

MECHANICAL ENERGY OSCILLATIONS DURING LOCOMOTION IN THE HARVESTMAN *LEIOBUNUM VITTATUM* (OPILIONES)

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ABSTRACT. The long legs, compact body and hanging posture of many harvestmen are unique among terrestrial animals, but no quantitative analyses of locomotion have been conducted to determine if this extreme morphology is associated with novel mechanisms of locomotion. Here we have undertaken a three-dimensional kinematic analysis of running *Leiobunum vittatum* (Say 1821) using field-by-field analysis of high-speed video. The center of mass of harvestmen was found to undergo vertical and transverse displacements of unprecedented magnitude, but the pattern of displacements was consistent with those predicted by general models of energetic efficiency and dynamic stability of pedestrian locomotion. Because these models assume substantial roles for elastic energy storage in leg elements, elasticity is probably an important component of the locomotor mechanism in harvestmen, and we identify two skeletomuscular elements as possible springs.

Keywords: Kinematics, elastic mechanisms, running, leg springs

Many harvestmen have exceptionally long legs, compact bodies and an ability to move rapidly on structurally complex horizontal and vertical surfaces. Yet, the kinematics of these common and familiar animals has never been described quantitatively let alone compared to that of more well-studied arthropods and vertebrates. Here we describe locomotion of a common “daddy longlegs,” *Leiobunum vittatum* (Say 1821), by examining the three-dimensional kinematics of animals running on a smooth, horizontal surface. We conclude that harvestmen use the same basic locomotor mechanisms as other pedestrian animals, although their unusual morphology significantly amplifies the sinusoidal vertical and transverse displacements of the body during locomotion. Specifically, we find that forward kinetic energy fluctuates in phase with potential energy as predicted by the spring-loaded inverted-pendulum model, which maintains that elastic energy is stored at one phase of the step cycle and converted to kinetic energy in a subsequent phase (Cavagna et al. 1977; Heglund et al. 1982; Alexander 1984, 1988; McMahon 1985, 1990; Farley et al. 1993; Full & Farley 2000). We also observe that fluctuations in

forward velocity of the center of mass occur at roughly twice the frequency of fluctuations in the transverse (lateral) velocity, a pattern consistent with that predicted by the lateral leg-spring model, which invokes elastic leg elements as a mechanism of passive (non-reflex) stabilization (Kubow & Full 1999; Schmidt & Holmes 2000a, b; Schmidt et al. 2002). These findings suggest that the legs of harvestmen act as springs in both the vertical and transverse axes that provide energetic efficiency and stability, respectively.

METHODS

Kinematics.—*Leiobunum vittatum* ($n = 6$ males, mass 50 ± 3 mg) (all values are mean \pm SE unless otherwise noted) were captured in a wooded area in College Park, Maryland, USA in August 2002 and were used in experiments within 24 h. Voucher specimens were deposited in the Denver Museum of Nature & Science, Denver, CO. Animals were induced to run on a smooth non-slip horizontal surface in the laboratory. They ran using stride frequencies between 3.6–5.2 Hz for several seconds when disturbed but favored lower speeds at other times. Images of fast-running

animals were captured using two synchronized (gen-locked) Peak Performance video cameras (120 fields/s) positioned to obtain lateral and dorsal perspectives. The angle between the cameras was about 90°. Videotapes were synchronized using a Peak Performance manually operated event marker. A calibration frame (4 cm × 4 cm × 4 cm) was videotaped by both cameras and filled most of the two fields of view. The frame consisted of 12 non-coplanar points. The resolution of points of the calibration frame was about 0.2 mm. Points in space could be located with mean-squared errors of 0.12 mm, 0.26 mm, and 0.15 mm for the x, y, and z positions, respectively, yielding a 0.32 mm mean-squared error for position.

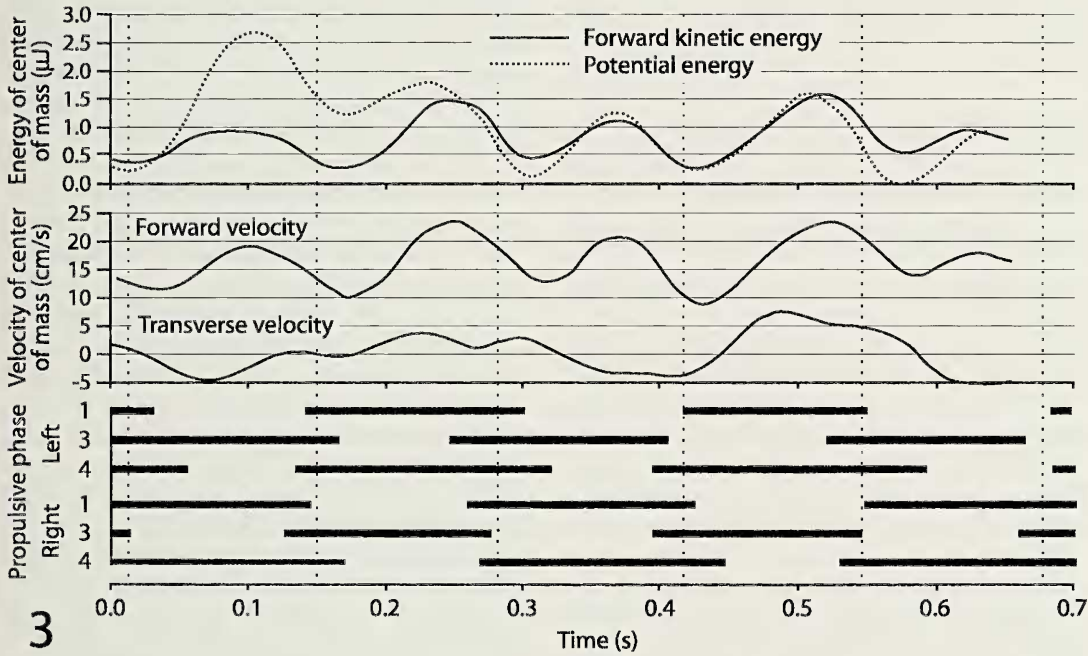
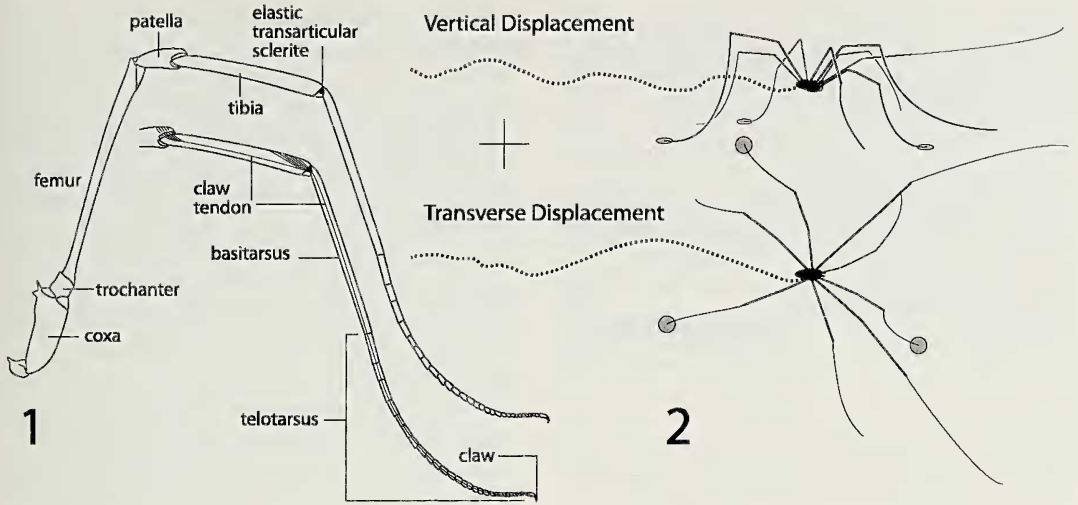
Videotapes were analyzed using a computerized motion analysis system (Motus, Peak Performance Technologies, Inc., version 6.0). The field of view was such that about two complete strides of each animal were captured during a run. A sequence was analyzed only if it was not interrupted by pauses or obvious changes in speed. The center of the body, distal end of the tarsus, tibia-tarsus joint, and femur-patella joint (Fig. 1) were digitized manually. Data from both cameras were treated using a low-pass, fourth-order, zero-phase-shift Butterworth digital filter with a cutoff-frequency of 10 Hz (Biewener & Full 1992) before direct linear transformation to three-dimensional coordinates. The overall animal center of mass was calculated for each field and incorporated the body and the center of mass of each effective leg segment.

Mechanical energy.—Masses of the body and effective leg segments were obtained by freezing specimens at 0° C for 30 min. Because the patella was short and essentially immobile relative to the tibia, the patella and tibia were treated together as one effective leg segment. Each leg was severed at the tibia-tarsus, femur-patella, and coxa-trochanter joints and each effective leg segment was weighed to the nearest μg (ATI-CAHN C-33 balance). Estimates of mechanical energy were derived from kinematic and mass measurements (Kram et al. 1997). The body constituted $73.0 \pm 0.8\%$ of total mass. When leg segments were taken into account, the overall center of mass was indistinguishable from the center of the body, except in the vertical axis, where the center of mass was located 0.5–2.0

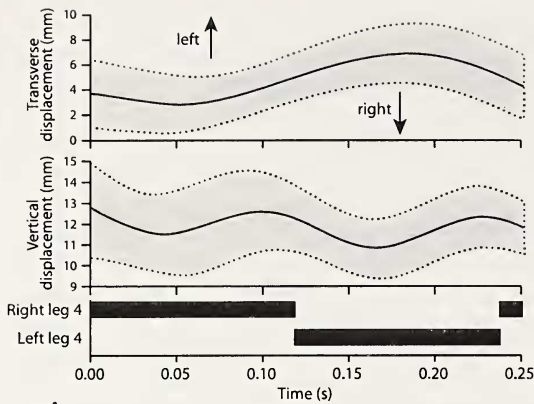
mm above the body. The center of the body was considered a sufficiently close approximation of the overall center of mass for use in calculations. Potential energy of the center of mass was calculated as mgh , where m was animal mass, g was gravitational acceleration, and h was height of the center of mass relative to the substratum. Forward kinetic energy of the center of mass was calculated as $\frac{1}{2}mv^2$ where v was velocity of the body. Total mechanical energy is the sum of kinetic and potential energy. Translational kinetic energies of the effective segments of leg 4 was calculated as $\frac{1}{2}mv^2$, where m was the mass of the effective leg segment and v was the velocity of the center of mass of the effective segment relative to the body. The rotational kinetic energy of each effective leg segment was calculated as $\frac{1}{2}I\omega^2$, where I was the inertia of the effective segment about its center of mass and ω was the angular velocity of that segment in a global coordinate system. The moment of inertia for each effective segment was approximated by $(1/12)ml^2$, where l was the length of the segment, which assumed each segment to be a slender rod of uniform density. Total limb kinetic energy was estimated by summing the translational and rotational energy fluctuations of the segments of leg 4 during a stride and multiplying by eight the total number of legs. This estimate was justified due to the similar shape and mass of the eight legs.

RESULTS

Kinematics.—Like other phalangid harvestmen, *Leiobunum vittatum* behaved as a functional hexapod, the antenniform second legs being used primarily as tactile organs. They used a hexapod-like alternating tripod gait, which provides a stable base of support throughout the locomotor cycle (Delcomyn 1985). Specifically, legs left 1, right 3 and left 4 moved essentially together as one tripod and moved out of phase with the tripod formed by legs right 1, left 3 and right 4 (Figs. 2, 3). At the onset of a step cycle, legs of one tripod contacted the substratum and members of the other tripod were lifted. At this point, the center of mass moved to its lowest level of 10 ± 0.4 mm or 1.7 ± 0.2 body lengths above the substratum. Retraction of leg 4 of a supporting tripod began at $16 \pm 1\%$ of the stride period before the lowest position of the center of mass was reached (Fig. 4). The center of mass



Figures 1-3.—1. Semi-diagrammatic retrolateral (posterior) view of the first leg of *Leiobum vittatum* showing basic anatomy and locations of possible spring-like mechanisms. 2. Body trajectory of a harvestman running at an approximate net speed of 17 cm/s from dorsal and lateral perspectives. Highlighted leg tips indicate the tripod of support. Scale bars = 1 cm. 3. An example of changes in kinetic and potential energy and in forward and transverse velocity in a harvestman running at an approximate net speed of 17 cm/s. The upper graph shows that forward kinetic and gravitational potential energy of the center of mass fluctuate in phase, as predicted by the spring-loaded inverted-pendulum model. The middle graph shows fluctuations in forward and transverse velocity of the center of mass. Note that negative velocities indicate transverse velocities when the center of mass is left of the net axis of travel and positive values are used when the center of mass is on the right. The pattern is roughly consistent with predictions of the lateral-leg-spring (LLS) hypothesis. The lower graph shows the stepping pattern (alternating tripod gait), with periods of support indicated by dark bars. Vertical dotted lines indicate the approximate point at which one tripod of support shifts to the other.



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Figure 4.—Average and SD of the center of mass position of running harvestman. Displacement over 1 stride from four individuals was normalized to step period (Motus, Peak Performance Technologies, Inc., version 6.0).

then moved upward to 13 ± 0.4 mm (2.2 ± 0.2 body lengths) as leg 4 of the supporting tripod appeared to push the body over the set of “crutches” formed by legs 1 and 3. Significantly, the plane of extension of leg 4 was not parallel to the overall axis of travel, and the center of mass was displaced transversely toward the side opposite the extending leg by 4.7 ± 0.4 mm (0.8 ± 0.2 body lengths). This mechanism resulted in a lurching motion with instantaneous forward velocity of the center of mass varying almost sinusoidally from 15–25 cm/s when the animal ran at an average speed of 20 cm/s (30.3 body lengths/s) (Figs. 2, 3).

Mechanical energy.—Forward kinetic and potential energy of the center of mass changed approximately in phase, with the average phase difference being less than the video time resolution. Vertical excursion of the center of mass in *L. vittatum* spanned slightly less than one body length, such that changes in potential energy (1.1 ± 0.10 μ J) were about twice that of the corresponding changes in kinetic energy (0.7 ± 0.06 μ J). Individual legs were 2.8–4.2% of total body mass. The kinetic energy associated with stopping and starting leg 4 during a stride was 0.020–0.025 μ J, with about 14% of this energy due to rotation of the segments. Assuming that kinetic energy of all legs was similar to leg 4 at observed running velocities, the magnitude of the limb kinetic energy oscillations was 9–

15% of the mechanical energy oscillations of the center of mass.

DISCUSSION

Significance of vertical fluctuations of the center of mass.—Comparative studies of legged locomotion in arthropods and vertebrates have revealed patterns of movement that transcend leg number, body size and phylogenetic distance (Full & Koditschek 1999; Blickhan & Full 1993; Farley et al. 1993; Full & Farley 2000). Cyclical changes in the vertical position of the body’s center of mass is one such pattern and is hypothesized to increase overall energetic efficiency through the interchange of kinetic and gravitational potential energy. The inverted pendulum (IP) model (Cavanga et al. 1977) applies to an animal moving forward while vaulting over a stiffened leg, as exemplified by a person using a pair of crutches. In the initial part of the step cycle, some kinetic energy used in moving the animal forward also raises the center of mass and increases gravitational potential energy. As the center of mass falls, potential energy is converted into kinetic energy, some of which can be used in initiating the next step cycle. The IP model predicts that changes in potential and forward kinetic energy occur 180° out of phase. Significantly, behavior consistent with the IP model has never been observed in arthropods and was not observed in *L. vittatum*.

In the spring-loaded inverted-pendulum (SLIP) model (Cavagna et al. 1977; Heglund et al. 1982; Alexander 1984, 1988; McMahon 1985, 1990; Farley et al. 1993; Full & Farley 2000), elastic elements in the legs serve as mechanisms of transient energy storage. Specifically, as the center of mass descends under the force of gravity elastic elements in the legs (that is, tensed muscles, tendons, and skeletal structures) are deformed, and forces produced by subsequent elastic recoil of these elements are used to propel the center of mass upward and forward to initiate a new cycle. In contrast to the IP model, the SLIP model predicts that forward kinetic and gravitational potential energy fluctuate in phase. The SLIP model matches locomotion in many vertebrates (Biewener et al. 1981; Alexander 1984; Farley et al. 1993), crabs (Blickhan & Full 1987), and cockroaches (Full & Tu 1990). Our observations of *L. vittatum* were also consistent with the SLIP model, and this species is the

least massive animal in which the predictions of the model have been met.

Significance of transverse displacements in the center of mass.—The magnitude of the transverse displacements of the center of mass observed in running *L. vittatum* (peak-to-peak displacement of 0.78 body lengths) (Figs. 2–4) are unprecedented. By comparison, the center of mass of the cockroach *Blaberus discoidalis* deviates laterally from the net axis of travel by less than 0.4 mm or 0.01 body lengths (Full & Tu 1990). The existence of substantial transverse accelerations of the body would seem to be energetically inefficient (Manton 1977) in the absence of a mechanism analogous to the SLIP model. Recent work suggests that cyclical transverse displacements are associated with a passive spring-based mechanism of directional stabilization that can respond to external perturbations to forward locomotion more rapidly than reflexes (Kubow & Full 1999; Schmidt & Holmes 2000a, b; Schmidt et al. 2002). Specifically, when a running animal experiences a transverse perturbation to the center of mass (wind, uneven substratum, another animal, etc.), leg springs could potentially absorb the energy and thereby prevent significant deviation from the net axis of travel. Some of this stored energy could also be converted to transverse kinetic energy upon elastic recoil and stored transiently by elastic elements in the legs on the opposite side of the animal. Theoretically, it is possible that energy from a brief transverse perturbation could be dissipated by elastic mechanisms over several strides while the center of mass oscillates along the net axis of travel.

The lateral-leg-spring model (LLS) of stabilization makes specific predictions about the timing of forward and transverse fluctuations of the center of mass (Kubow & Full 1999; Schmidt & Holmes 2000a, b; Schmidt et al. 2002). Specifically, velocities of forward and transverse displacement are predicted to vary sinusoidally during locomotion, with peak forward velocity occurring in phase with peak rightward and leftward transverse velocities. When transverse velocity of the center of mass is assigned negative values whenever the center of mass deviates to the left of the net axis of travel and positive values when to the right (as in Fig. 3), the wavelength of transverse velocity should be twice that of forward

velocity. Kinematic analysis of the cockroach *Blaberus discoidalis* largely corroborates predictions of the model (Schmidt et al. 2002).

Kinematics in running *Leioibunum* was also roughly consistent with the LLS model (Fig. 3). Specifically, the transverse-velocity sinusoid has a wavelength about twice that of the forward velocity and the peaks and troughs of the transverse velocity plot occur near the peaks in forward velocity. However, in contrast to the fairly simple sinusoid displayed by forward velocity, transverse velocity showed a more complex pattern and may even have had a low-amplitude, short-wavelength velocity fluctuation superimposed on the predicted waveform. In addition, peaks in the transverse waveform appeared to precede peaks in forward velocity rather than occurring simultaneously as predicted. Significantly, the phase difference between the forward and transverse velocity peaks was also observed in the cockroach (Schmidt et al. 2002: fig. 6). The overall similarity of the predictions of the LLS model and empirical observations indicate that lateral springs are probably important for locomotion and specifically for stabilization. However, given that two arthropods deviate from expectations in the same manner, the LLS model probably needs refinement.

Locations of possible leg springs.—Compatibility of locomotor kinematics with the SLIP and LLS models indicate that elastic energy storage is a significant component of locomotion in *L. vittatum*, but the anatomical placement of appropriate elastic mechanisms is not known. The existence of highly efficient springs has already been documented at the tibia-tarsus joint in *L. vittatum*, although its precise role in locomotion has yet to be determined (Sensenig & Shultz 2003). The tibia-tarsus joint of each leg is spanned by a pair of deformable sclerites that store energy during flexion and return up to 90% of this energy during extension. Gravity can potentially assist muscles in deforming the elastic sclerites of legs 1 and 3 during locomotion, but flexion of this joint in leg 4 occurs only when the leg is off the ground and it is unlikely that the sclerites could be loaded by gravity.

In principle, any muscle-tendon complex can store externally generated mechanical energy if its contractile and/or connective elements have intrinsic tensile resilience and experience externally generated tensile forces

(McMahon 1990). Shultz (2000) identified 13 intrinsic leg muscles in *Leiobunum*, but the muscle-tendon complex of the claw (Fig. 1) seems particularly well suited to act as a spring. Here a long tendon attaches to the claw distally, spans the length of the multi-segmented tarsus, and attaches proximally in the tibia and patella via muscles (Guffey et al. 2000; Shultz 2000). The tarsus is typically curved when supporting the animal, both when standing and during locomotion (Fig. 2). Forces from gravity, propulsive movements or transverse perturbations during locomotion may bend the tarsus further, thereby increasing tension on the muscle-tendon complex and storing energy within its elastic elements. Elastic energy might then be converted to kinetic energy toward the opposite direction once the tensile load was released causing the tendon to shorten and the tarsus to "unbend." A comparable mechanism exists in other arthropods, where elasticity of the tarsal tendon maintains postural equilibrium in the face of external perturbation (Frazier et al. 1999). However, determining the precise role of the claw tendon and other potentially elastic elements in *Leiobunum* will require additional investigation.

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